Paleoecology of the Calceocrinidae with a Description of New Material from the Brassfield Formation (early Silurian)

A Thesis

Presented in partial fulfillment of the requirements
for the degree of Bachelor of Science
in Geological Sciences

by

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July 2007

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ABSTRACT

The Calceocrinidae is the longest ranging crinoid family, from the middle Ordovician to the early Permian. Unique morphology led to a mode of life that proved to be successful for approximately 230 million years. Many life models have been suggested for the calceocrinids. However, they are interpreted to be leeward passive suspension feeders that thrived in a number of environments throughout the Paleozoic. During the Ordovician, calceocrinids were best adapted to shallow-water carbonate platforms. During the Silurian and Devonian, calceocrinids preferred shallow-water carbonate platforms, however, they adapted to a wider array of habitats. During the early Mississippian, calceocrinids abandoned shallow-water carbonate platforms and moved to a deeper-water siliciclastic regime. The purpose of this study is to reexamine the paleoecology of the Calceocrinidae, focusing on their life modes and paleoenvironments. Further, new material from the early Silurian, Brassfield Limestone of Ohio and Kentucky is described.

ACKNOWLEDGMENTS

It is my pleasure to acknowledge my thesis advisor, Professor William I. Ausich, for his materials and assistance throughout my undergraduate research. I would like to thank The Ohio State University's Earth Sciences program for their dedication and guidance over the last few years. I would also like to acknowledge the staff of the Orton Geologic Library for their assistance with locating resources for my thesis. Lastly, it brings me much pleasure to pay attributes to my family for their support and guidance throughout the years. To my mother, Patricia L. Boyarko, and my sister, Chandler L. Boyarko, I dedicate my works to them for their strength, inspiration, and love.

INTRODUCTION

Calceocrinids first appeared in the rock record in the late Ordovician (Blackriverian, Llanvirn). They are known from the Silurian to the late Devonian, where they do not reappear until the early Mississippian. During the early Mississippian, they leave the rock record and do not occur again until the early Permian (Leonardian, Artinskian). The family Calceocrinidae is characterized by being morphologically divergent from the rest of the Crinoidea. The development of a hinge that articulates the basal and radial circlets, the change from a five to a three- or four-arm body plan, and the reduction of radial and or basal plates led to a bilaterally symmetric crown with a highly modified cup and arms (Moore 1962). These changes in morphology led to an alternative lifestyle that was undoubtedly successful, as they are the longest lived family of crinoids.

Modern crinoids are known to suspension feed with the column erect from the substrate, thereby elevating the crown and opening their arms into a filtration fan. The fan collects nutrients from the water column along an ambulacral groove system located on the oral side of the arms. Traditionally, crinoids elevate the crown into or above the benthic boundary layer in order to get into a zone with higher currents and food resources. The calceocrinids deviated from this lifestyle by feeding with their column recumbent along the substrate, and the crown oriented nearly perpendicular to the current, the runner mode. This lifestyle proved advantageous for the calceocrinids. By living near the bottom of the benthic boundary layer, there would be less competition for feeding space among crinoids. In addition, the development of the hinge between the basal and radial circlets would allow the calceocrinid to move from a feeding position to a closed position as a defensive mechanism to predation and high sedimentation.

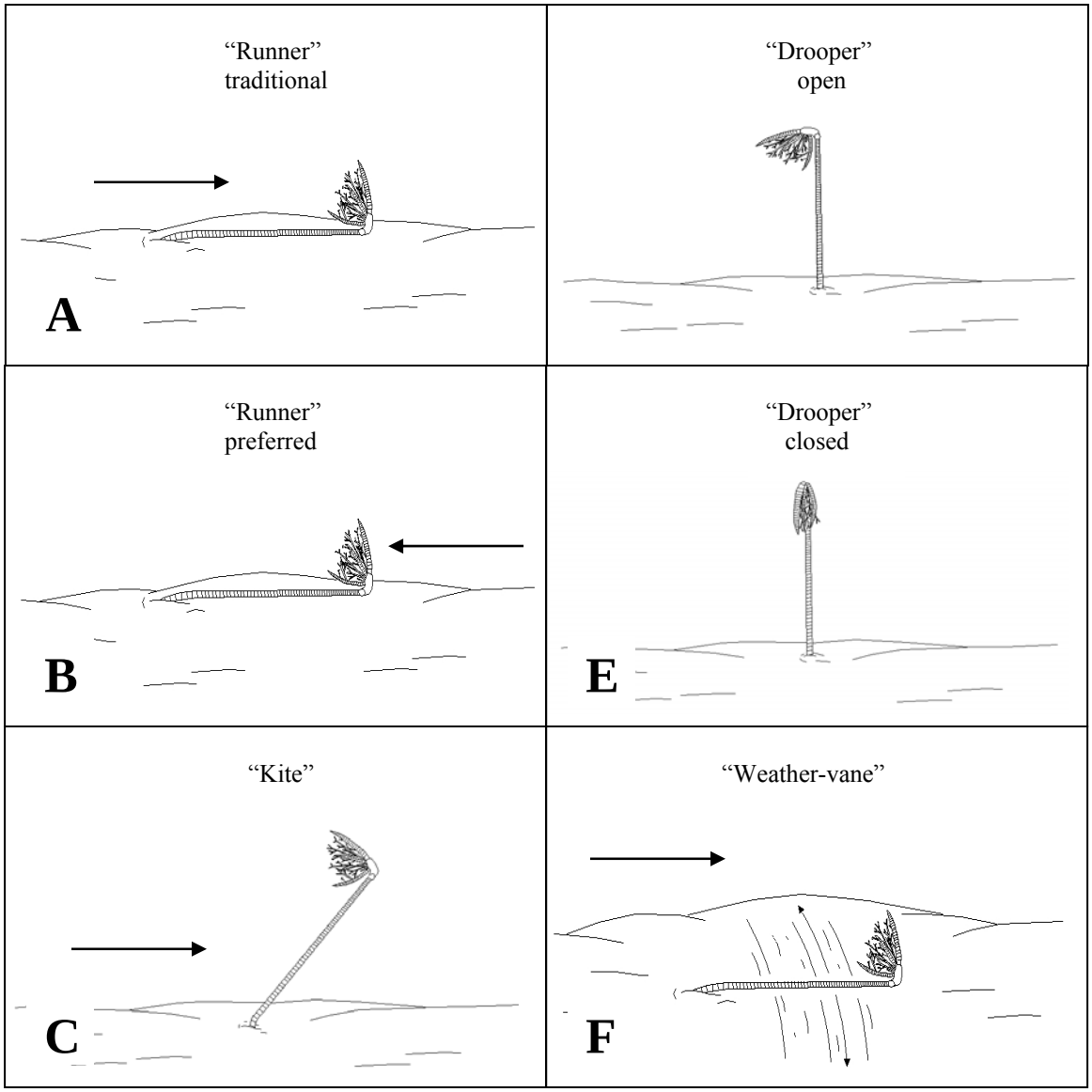
Calceocrinids are known from a number of paleoenvironments from shallow-water carbonate platforms to deep-water siliciclastic settings throughout the Paleozoic. The purpose of this study is to investigate the spatial and temporal history of the Calceocrinidae and to describe new material from the early Silurian of Ohio and Kentucky.

LIFE MODES OF THE CALCEOCRINIDAE

The calceocrinids deviated from the normal life mode of stalked crinoids with their unique morphology. Modern crinoids live on the seafloor or by attachment to some object in which their stem is erect, and the arms are displayed into a filtration fan to feed from the passing current. Changes in the morphology of the calceocrinids were the development of a hinge located between the basal and radial circlets, the subtraction of a basal and/or radial plate, and a reduction to three or four arms. The hinge allowed for the animal to move from a recumbent to a feeding position, or vice-versa. Analyzing the functional morphology has led to several models for the life modes of the calceocrinids. The following autecological models have been proposed and will be further discussed: 'runner' (Jaeckel 1918), 'kite' (Breimer and Webster 1975), 'weather-vane' (Kesling and Sigler 1969), and 'drooper' (Ringueberg 1889).

The runner model (TEXT-FIG 1 A) was suggested by Jaeckel (1918) and has received wide support form the paleontological community (Ausich 1986). The column of the calceocrinid would have lain parallel to the substrate, and the crown would be either held vertical to the substrate for feeding or horizontal along the column in a closed position. In the closed position, the arms of the crinoid would lie over the column keeping the ambulacral grooves protected from outside influences. In the feeding position, the hinge would be open, the crown would be oriented nearly perpendicular to the column, and the arms would fan out into a feeding posture.

The kite model (TEXT-FIG 1 C) was suggested by Breimer and Webster (1975) and is a variation to the runner mode. However, in this model the current is able to give sufficient lift to the crown to elevate it from the substrate during feeding.



TEXT-FIG 1. Various reconstructions of autecological life modes for calceocrinids. Arrows indicate current direction. A, traditional runner mode with the currents striking the oral surface of arms (Jaeckel 1918, Ausich 1986); B, preferred runner mode with the currents striking the aboral surface of arms (Ausich 1986); C, kite mode, a variation of the runner mode in which the crown is elevated off the seafloor (Breimer and Webster 1975, Ausich 1986); D, E, drooper mode, analogous to the life mode of modern stalked crinoids (Ringueberg 1889, Ausich 1986); F, weather-vane mode, a variation to the runner mode in which the crown is able to reorient itself with the current by lateral movements along a pivot (Kesling and Sigler 1969, Ausich 1986).

The weather-vane model (TEXT-FIG 1 F) was suggested by Kesling and Sigler (1969) and represents another variation of the runner model in which the holdfast of the calceocrinid allowed for reorientation of the crown so as to maintain the best feeding orientation with respect to the current.

The drooper model (TEXT-FIG 1 D, E) was suggested by Ringueberg (1889) and is analogous to the life mode of modern stalked crinoids. Modern stalked crinoids spend their lives with the column erect above the substrate as would the calceocrinids in this life mode. However, in the feeding position, a drooper's crown would be oriented nearly perpendicular to the column. In a closed position, the crown would rest parallel along the column.

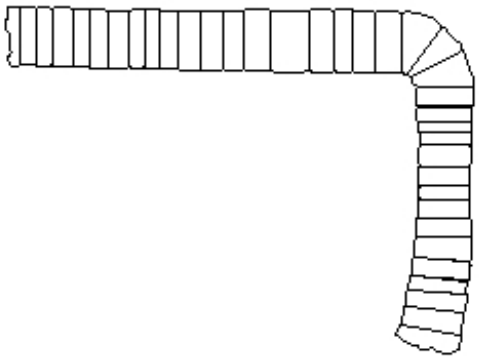
DISCUSSION OF THE LIFE MODES OF THE CALCEOCRINIDAE

The morphology of the calceocrinids clearly dictates an unusual life mode compared to most crinoids. However, this change was very successful. The Calceocrinidae is the longest ranging crinoid family, from the middle Ordovician to the early Permian, approximately 230 million years. The autecological life mode that makes the most sense and has received the most support is the runner mode.

Ringueberg proposed that calceocrinids lived with the column projected vertically from the seafloor, in the drooper mode. However, hydrodynamic and morphological evidence does not support this theory. Hydrodynamically, filter-feeding would not be maximized using the drooper mode because the fan orientation would not be in a position perpendicular to the current. In an open position, the orientation of the fan would be at an oblique angle to the current, reducing the area that the fan could filter. In fact, the only way the calceocrinid would be able to maximize the fan with respect to the current would be to stay closed, which would make an inefficient filter at best. It seems unlikely that the calceocrinids lived in an erect manner as other stalked crinoids. The drooper model does not have any advantages that would benefit the calceocrinids change in morphology. In fact, this mode would be very disadvantaged with respect to feeding.

Also critical for the drooper mode is the calceocrinid stem length that would need to be longer than the arm length in order to keep the arms from swaying in the sediment while in a resting position. Such an action could easily disturb the ambulacral system in the arms of these animals.

Brower (1966) reported an unknown species of *Calceocrinus* with a crown length of 19 mm and a stem length of 6.5 mm. Next to the distal part of the stem was a holdfast which belonged to the specimen. Brower (1977) described two complete specimens from the Bromide Formation in which the arm length was greater that the stem length. Springer (1926) also reported short-stemmed calceocrinids in which attachment was to foreign objects. As recognized, most of the known calceocrinid specimens have much longer stems than arms (Ausich 1986). However, Brower (1966, 1977) and Springer (1926) interpreted that these specimens must have lived with their column recumbent along the seafloor, indicating a runner life mode.



TEXT-FIG 2. *Trypherocrinus brassfieldensis*, USNM 351853, ×5.4. Reconstruction of oblique view of distal column (Ausich 1986).

In addition, Ausich (1984) described an *in situ* holdfast of *Trypherocrinus brassfieldensis* in which the distal part of the column projected vertically from the substrate and was redirected nearly parallel to the substrate by a series of wedge-shaped

columnals (TEXT-FIG 2). Brett (1981, 1985) also described holdfast and column relations indicating the calceocrinid column would have lain recumbent along the seafloor. At least in the cases listed above, the column must have lain along the seafloor in a recumbent posture, therefore, dictating that these calceocrinids did not assume in a drooper life mode.

Kesling and Sigler (1969) proposed that the calceocrinids lived along the seafloor in a version of the runner mode, the weather-vane mode. In this life style, the column would be able to move laterally along a pivot, i.e. the holdfast-column articulation, in order to reorient the fan with the current. However, no known articulation between the holdfast and the column would allow such a rotation (Ausich 1986). Ausich (1986) also mentioned that Eckert (1984) proposed that the holdfast-column articulations in many crinoids are at a steep angle, reducing the amount of rotation between the holdfast and the column.

Breimer and Webster (1975) proposed that the calceocrinids lived along the seafloor in a version of the runner mode, the kite mode. In this life mode, there would be three positions in which the hinge would function: the “normal” closed runner, the “normal” feeding runner, and an “elevated” feeding runner. They hypothesized that by orienting the crown in an oblique fashion with respect to the current, the passing current would provide sufficient lift to elevate the crown off of the seafloor in the “elevated” feeding runner position. The lift from the current would have to have been sufficient to lift the weight of the crown, but the locking of the columnar ligaments is thought to have maintained the “elevated” position (Breimer and Webster 1975). Brower (1977) noted that not all calceocrinids would function in this manner. Special hydrodynamic and

morphological requirements would need to be met in order to gain such a lift. Morphologically, the crown would need to be light, the arms would need to be complex with heterotomous branching, and the stem length would need to be long. Baumiller (1992) studied the process of hydrodynamic lift in modern isocrinids and calceocrinids. Hydrodynamically, the passing current would have to be very strong to provide any lift at all, indicating that if this life mode were to be plausible, these animals would need to live in high energy environments. Baumiller (1992) concluded that under normal conditions, crinoids could not function as kites; however, hydrodynamic lift could be used for reorientation as a response to current direction changes, a mechanism to elevate the crown above the substrate, following dislodgement or crawling, and a mechanism to achieve a normal feeding posture.

With respect to the orientation to the current, Breimer and Webster's kite model and Kesling and Sigler's weather-vane model were proposed under the assumption that the calceocrinids fed with the oral side of the arms facing into the current. However, modern crinoids are known to be leeward passive suspension feeders, i.e., the oral side of the arms down-current (Macurda and Meyer 1974). It was proposed that the calceocrinids did not deviate from this style of feeding (Ausich 1986). With this the case, the arguments for the kite and weather-vane life modes are severely weakened.

Jaeckel proposed the calceocrinids lived along the seafloor in the runner mode in which the column was recumbent along the substrate. In this feeding position, the crown would be nearly perpendicular to the column and the current maximizing the fan's surface area from which it could feed and making it a more effective filter-feeder. In addition, with the hinge in a closed position, the arms would lay parallel to the column in

a manner in which the oral side of the arms would be protected from outside influences. This position would allow as a defense system from periods of high sedimentation as well as a defense against predators.

Jaeckel proposed the runner model under the assumption that the calceocrinids fed with the oral side of the arms up-current (traditional orientation to current). However, like modern crinoids, the "preferred" orientation (TEXT-FIG 1 B) to the current would be with the current striking the aboral sides of the arms (Ausich 1986). With this orientation to the current, stronger currents would be less likely to injure the animal. Baumiller (1992) noted that under specific conditions, i.e., strong currents and the traditional orientation to the current, the horizontal forces acting on crinoids could be great enough to deflect the stalk or even tear the animal from its attachment. However, calceocrinids living with the preferred orientation to the current would be able to adjust to violent currents. The horizontal forces of the currents could be used to assist the movement of the crown from a feeding posture to recumbent along the column.

The "preferred" runner mode with the current striking the aboral side of the arms would have been the most advantageous life mode for the calceocrinids with respect to their morphology and the hydrodynamics of the ocean. In the runner mode, the calceocrinids would be able to expend a minimal amount of energy, maximize filter-feeding, and be readily available for defense. Therefore, the most likely explanation of how calceocrinids lived would have been as leeward passive suspension feeders.

DIVERSITY DECLINES AND THE PALEOENVIRONMENTAL DISTRIBUTION OF THE CALCEOCRINIDAE

Materials and method.– Data was collected from Webster (2003), primarily for known stratigraphic occurrences of calceocrinids and the Paleobiology Database, primarily for paleoenvironment interpretation of known stratigraphic occurrences. Data from the Paleobiology Database were downloaded for calceocrinid genera during June and July 2007. The final paleoenvironment interpretations were completed in consultation with Dr. William I. Ausich. The primary goal of the data collection was to examine the temporal distribution of calceocrinids and their paleoenvironments.

Ausich (1986) described five diversity declines of the Calceocrinidae: the middle to the late Ordovician, the late Silurian to the early Devonian, the middle Devonian to the early Mississippian, the early Mississippian to the early Permian, and the extinction following the early Permian. Specific causes for the declines are difficult to address.

The earliest known occurrence of the Calceocrinidae was during the middle Ordovician. Following the transition of the middle to late Ordovician, there was a decline in absolute calceocrinid diversity and a decline in the proportion of calceocrinids compared to all crinoids (Ausich 1986). Throughout the Ordovician, calceocrinids were best adapted to a shallow-water carbonate platform environment (TEXT-FIG 3). Further, they are known from deep subtidal ramp settings.

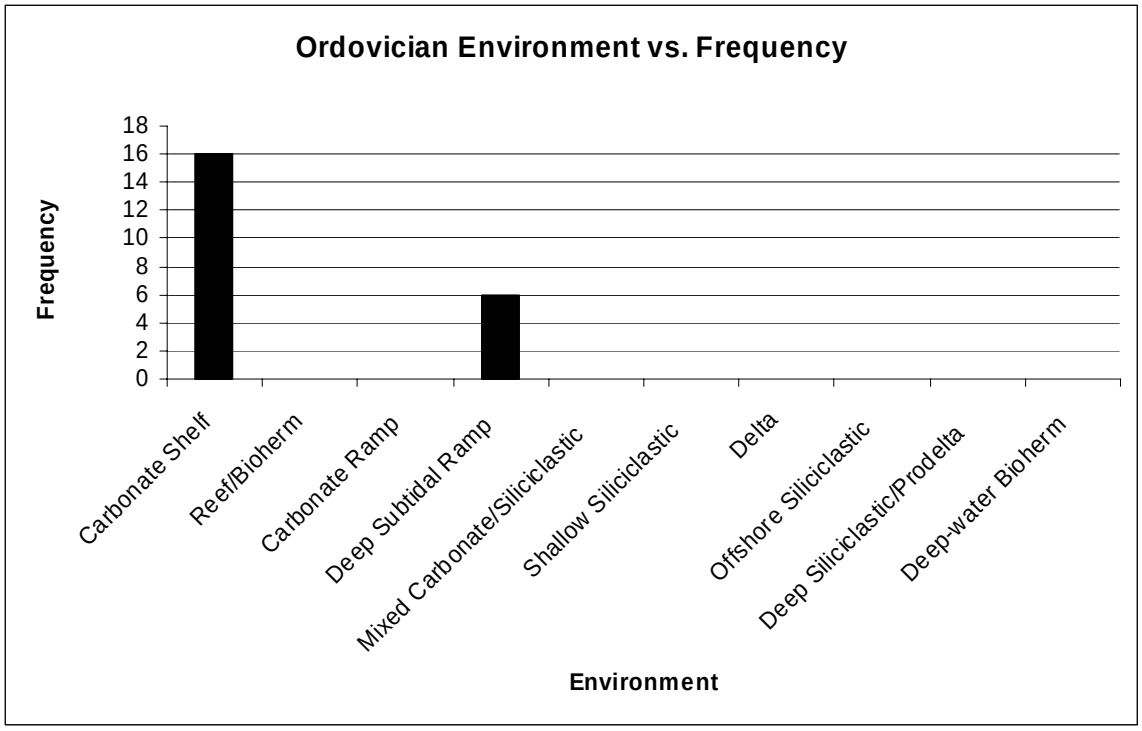
By the end of the early Silurian there was an increase in species diversity that similar to that of the middle Ordovician (Ausich 1986). Accompanying the increase in species diversity, calceocrinids occupied a much wider array of habitats (TEXT-FIG 4).

The calceocrinids were still best adapted to shallow-water carbonate platform settings, but reef and bioherm settings were also as favorable. Further, they are known to occur in deep subtidal ramp, mixed carbonate and siliciclastic, offshore siliciclastic, and prodelta environments.

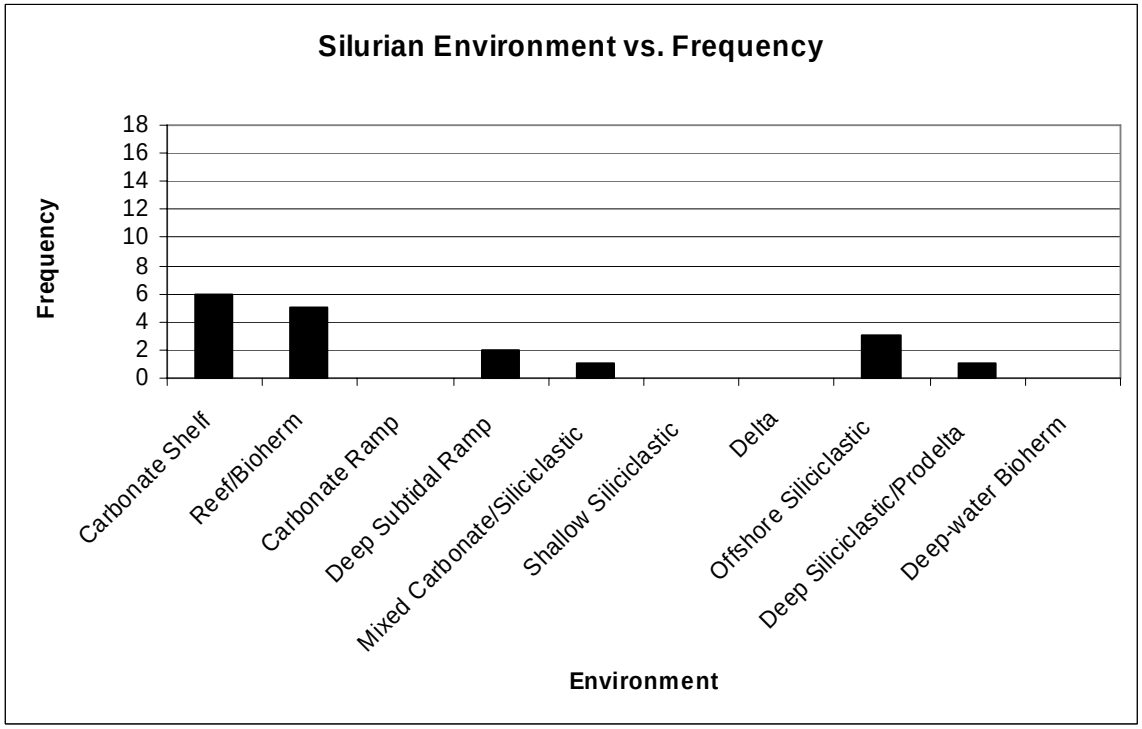
The transition from the late Silurian to the early Devonian was marked by a decrease in both numeric diversity and in relation to all crinoids (Ausich 1986). Environmental distributions of the calceocrinids throughout the Silurian and Devonian show no marked differences. Ausich (1986) offered biotic interactions of increased predation by fishes and other durophagus predators and competition for food and space by bryozoans as potential causes for the decline. Throughout the Devonian, calceocrinids were still best adapted to shallow-water carbonate platform settings (TEXT-FIG 5). However, they were still present in a wide array of habitats including reef and bioherm, deep subtidal ramp, mixed carbonate and siliciclastic, shallow siliciclastic, prodelta, and deep siliciclastic environments. Calceocrinids are not known from the late Devonian.

Calceocrinids reappear in the early Mississippian and are not observed again until the early Permian. During the Ordovician, Silurian, and Devonian, calceocrinids were best adapted to shallow-water carbonate platform environments. However, Mississippian calceocrinids are not known from such settings. They moved from shallow-water carbonate settings to a deeper-water siliciclastic environment (TEXT-FIG 6). Accompanying this shift in habitat is the marked decrease in genus-level richness in the Mississippian (Ausich 1986). Where present, early Mississippian calceocrinids may be very abundant, but all early Mississippian species belong to the genus *Halysiocrinus*.

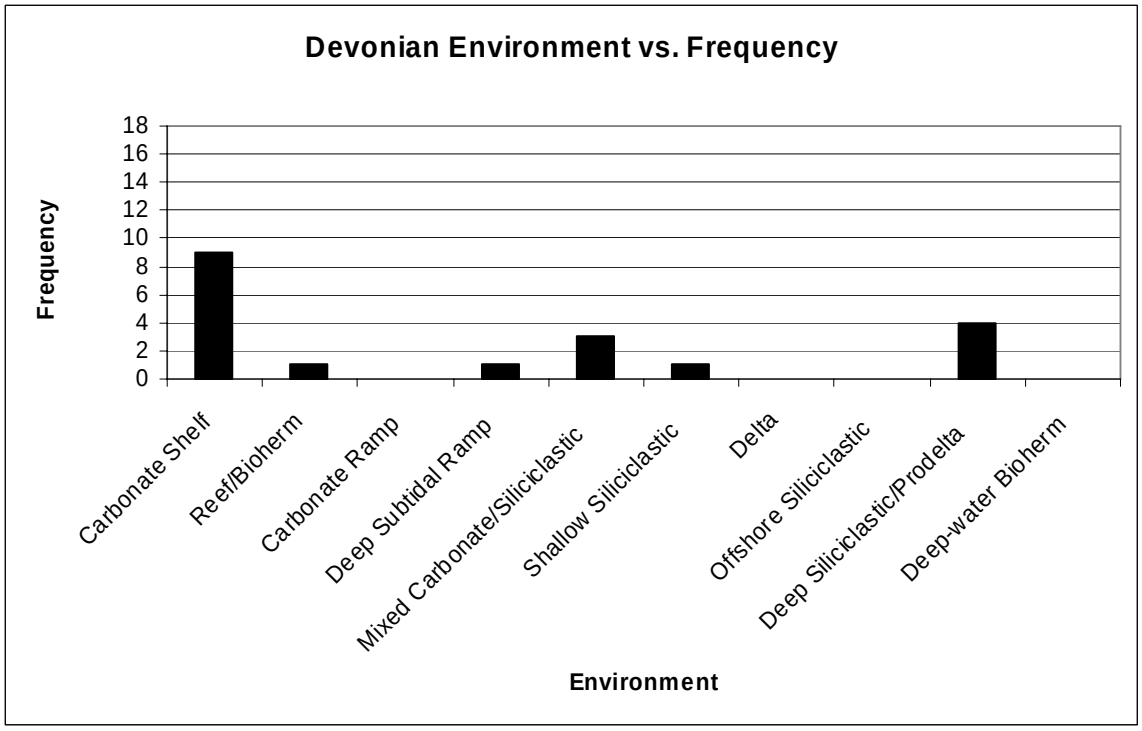
The calceocrinids reappear in the early Permian with a single occurrence. They are only known from an offshore siliciclastic environment. Only one genus and one species are known. The calceocrinids presumably became extinct after the early Permian.



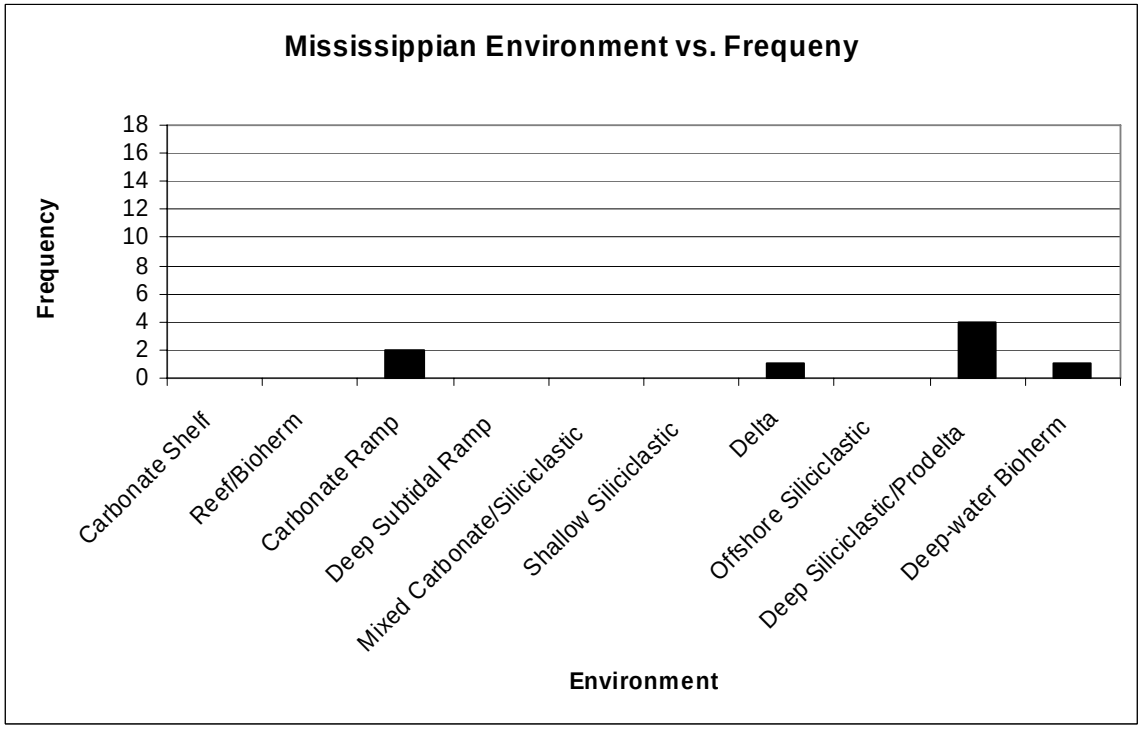
TEXT-FIG 3. During the Ordovician, calceocrinids preferred shallow-water carbonate platforms and are known from deep subtidal ramp environments.



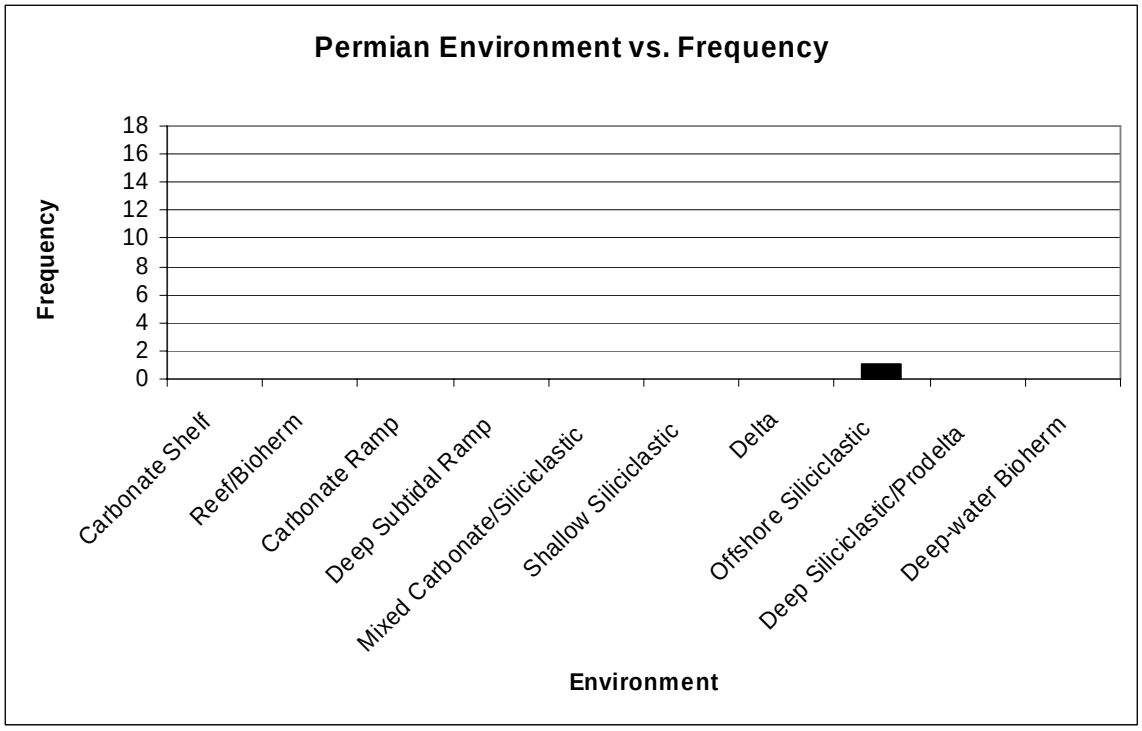
TEXT-FIG 4. During the Silurian, calceocrinids preferred shallow-water carbonate platform and reef/bioherm settings. They also started to make their way into a number of different environments.



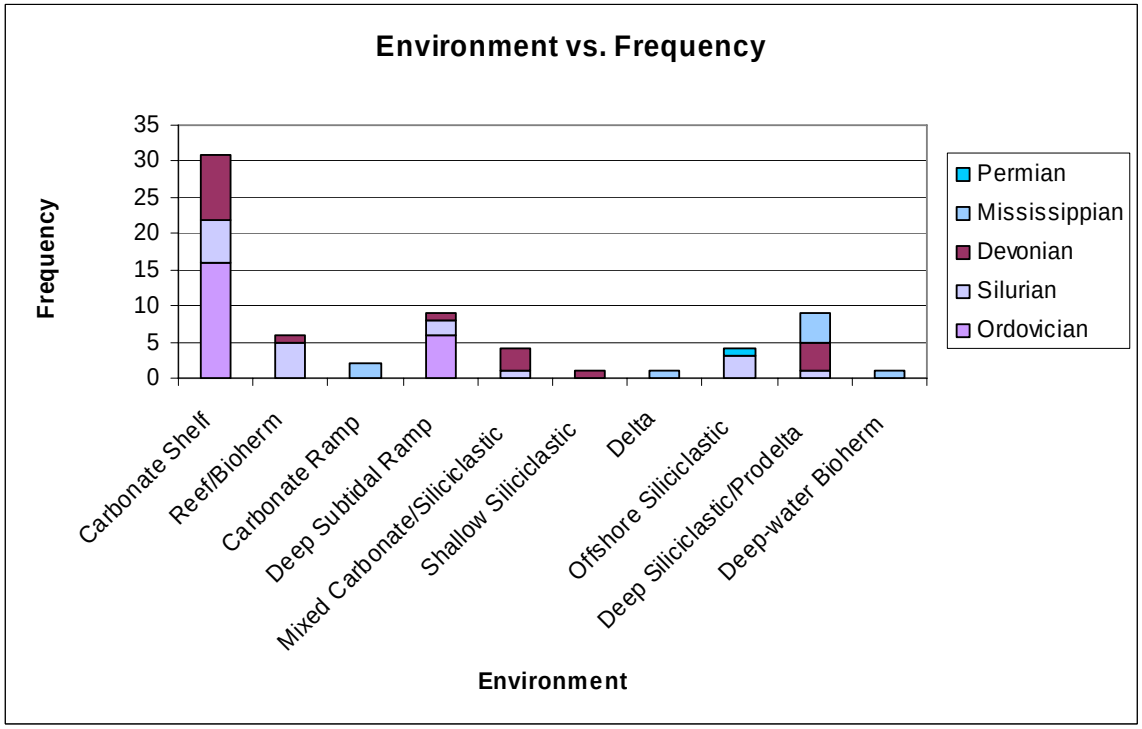
TEXT-FIG 5. During the Devonian, calceocrinids preferred shallow-water carbonate platforms and continued to exist in many other environments.



TEXT-FIG 6. During the Mississippian, the calceocrinids made a shift from shallow-water carbonate platforms to a deeper water siliciclastic regime.



TEXT-FIG 7. During the early Permian, the only known occurrence of the calceocrinids is from an offshore siliciclastic environment. The calceocrinids are not known after the early Permian.



TEXT-FIG 8. Stacked histogram of the Environment vs. Frequency for the calceocrinids from the middle Ordovician to the early Permian.

SYSTEMATIC PALEONTOLOGY

Class CRINOIDEA, Miller 1821
Subclass INADUNATA
Wachsmuth and Springer, 1885
Order DISPARIDA Moore and Laudon, 1943
Superfamily CALCEOCRINACEA
Meek and Worthen, 1869
Family CALCEOCRINIDAE
Meek and Worthen, 1869

Trypherocrinus adamsensis
n. sp.

Diagnosis.– Trypherocrinus adamsensis is distinct from *Trypherocrinus brassfieldensis* in the following ways. All plates are smooth. The anal X is supported beneath on one side by the B superradial and presumably on the other side by at least the C superradial. The anal X supports four known additional plates. The E-ray arm bifurcates on the fourth alphabrachial, third betabrachial, and fourth gammabrachial. Lateral arms with heterotomous branching. The primaxil arm bifurcates on the second alphabrachial, third betabrachial, third gammabrachial, and third deltabrachial. The secundaxil arm bifurcates on the third alphabrachial, third betabrachial, and third gammabrachial. The tetraxil arm bifurcates on the third alphabrachial, third betabrachial, and third gammabrachial. The omega arm bifurcates on the fifth and seventh alphabrachials. Proximal columnals are very thin.

TABLE 1. Measurements of *Trypherocrinus adamsensis* (in mm). HBC, height of basal circlet through plane of bilateral symmetry; WBC, width of basal circlet along distal margin; HRC, height of radial circlet through plane of bilateral symmetry; WRC, maximum width of radial circlet; HC, height of crown; LC, length of preserved column; *, incomplete; **, holotype.

Specimen	HBC	WBC	HRC	WRC	HC	LC
OSU 50496**	1.4*	–	5.0*	3.8*	24	17.6

Description.– The crown is relatively small, slender, and pendant on the stem. The aboral cup is relatively small, laterally compressed, and slender.

The basal circlet is broken, so its overall shape is unknown and other characters are difficult to confirm, but apparently three basal plates are present, including one triangular plate formed by the fusion of EA and DE basal plates that articulates with the radial circlet. The stem is equally supported by the AB and CD basals.

TEXT-FIG 9. *Trypherocrinus adamsensis*, holotype, OSU 50496, ×7 . Lateral view.

The radial circlet is laterally compressed and rectangular from aboral view. A and D radials comprise the majority of the radial plate circlet. Both the E inferradial and E superradial narrow in width toward the center of the radial circlet and form a connection.

The E superradial occupies the entire distal edge of the aboral cup and supports the E-ray arm. The upper lateral facet of the A radial supports the A lateral arm, and two lower lateral facets of the A radial support the B inferradial and B superradial.

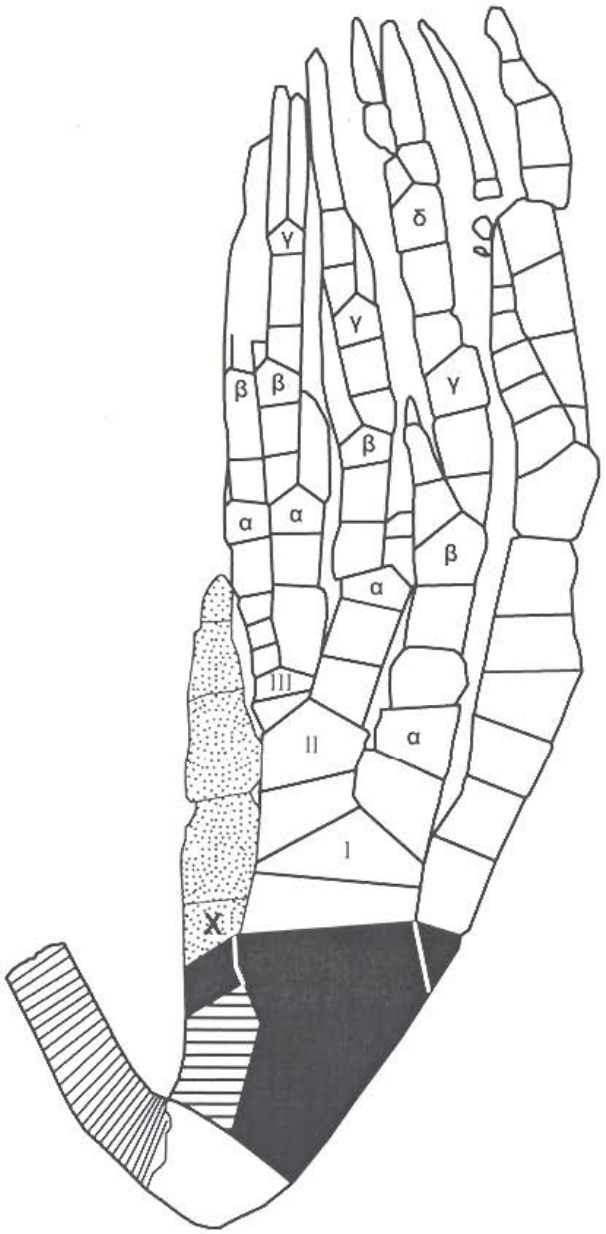
The anal X is a pentagonally shaped plate supported beneath on one side by the B superradial and presumably on the other side by at least the C superradial. The anal X supports four known anal plates, at least three of the proximal are rectangular. Consequently, the anal sac was probably very short and did not project above the E-ray first primibrachial.

Three arms are present. The E-ray arm is slender and branched with brachials of variable height. The fourth alphabrachial, third betabrachial, and fourth gammabrachial are axillary. The E-ray brachial height:width ratios vary from 1.5 to 1.

Lateral arms are characterized by weakly developed main axil series and by an arm branching pattern that deviates somewhat from the normal calceocrinid heterotomy. Three axillaries are present within the main axil with a non-axillary brachial beneath each. All bifurcations within the main axil and axil arms are isotomous or nearly so. In the traditional calceocrinid sense, three axil arms are present. Rather than the normal bilateral calceocrinid heterotomy in which unbranched ramules are alternately abaxially-adaxially borne along an axil arm, in *Trypherocinus adamsensis* Boyarko branching above at least the alphabrachial is nearly isotomous with a tendency toward adaxial heterotomy. Classification of arm axils follows Moore (1962). Axillaries of the axil arms are commonly much larger than non-axillary brachials.

The alpha ramule on the primaxil arm bifurcates on the second alphabrachial and supports the betabrachitaxis adaxially and the alpha ramule abaxially which is covered by

arms thereafter. The beta ramule bifurcates on the third betabrachial. The third betabrachial is axillary and supports the gammabrachitaxis abaxially and the beta ramule adaxially. Distally, the beta ramule continues with three known plates and is unseen thereafter. The gamma ramule bifurcates on the third gammabrachial and supports the



TEXT-FIG 10. *Trypherocrinus adamsensis*, holotype OSU 50496, ×6. Camera lucida drawing of oblique view; interpretation of plates: black, radials and superradials; horizontally ruled, inferradials; stippled, annals; X, anal X; arm designs from Ausich (1984).

deltabrachitaxis adaxially and the gamma ramule abaxially which is unseen thereafter. The delta ramule bifurcates on the third deltabrachial and supports the epsilonbrachitaxis abaxially and the delta ramule adaxially. Distally, the epsilon and delta ramules continue with two and three known plates, respectively, and are unseen thereafter.

The alpha ramule on the secundaxil arm bifurcates on the third alphabrachial and supports the betabrachitaxis adaxially and the alpha ramule abaxially. Distally, the alpha ramule continues with two known brachials and is unseen thereafter. The beta ramule bifurcates on the third betabrachial and supports the gammabrachitaxis abaxially and the beta ramule adaxially. Distally, the beta ramule is severely weathered continuing with at least one known plate and is unseen thereafter. The gamma ramule bifurcates on the third gammabrachial and supports the deltabrachitaxis adaxially and the gamma ramule abaxially. Distally, the gamma ramule continues with one known plate and is unseen thereafter, and the delta ramule continues with three known plates and is unseen thereafter.

The alpha ramule on the secundaxil arm bifurcates on the third alphabrachial and supports the betabrachitaxis adaxially and the alpha ramule abaxially. Distally, the alpha ramule continues with two known brachials and is unseen thereafter. The beta ramule bifurcates on the third betabrachial and supports the gammabrachitaxis abaxially and the beta ramule adaxially. Distally, the beta ramule is severely weathered continuing with at least one known plate and is unseen thereafter. The gamma ramule bifurcates on the third gammabrachial and supports the deltabrachitaxis adaxially and the gamma ramule abaxially. Distally, the gamma ramule continues with one known plate and is unseen

thereafter, and the delta ramule continues with three known plates and is unseen thereafter.

The alpha ramule on the tetraxil arm bifurcates on the third alphabrachial and supports the deltabrachitaxis adaxially and the alpha ramule abaxially. Distally, the alpha ramule continues with one known brachial and is unseen thereafter. The beta ramule bifurcates on the third betabrachial and supports the gammabrachitaxis abaxially and the beta ramule adaxially. Distally, the beta ramule continues with one known brachial and is unseen thereafter. The gamma ramule bifurcates on the third gammabrachial and supports the deltabrachitaxis adaxially and the gamma ramule abaxially. Distally, the delta and gamma ramules are severely weathered and continue with one known plate for each and are both unseen thereafter.

The omega ramule is branched, and normal axil arm terminology will be applied to this arm. The alpha ramule bifurcates on the fifth alphabrachial and supports the betabrachitaxis adaxially and the alpha ramule abaxially. Distally, the beta ramule continues with one known plate and is unseen thereafter. The alpha ramule continues and bifurcates on the seventh alphabrachial and supports the gammabrachitaxis adaxially and the alpha ramule abaxially. Distally, the arms are severely weathered and would presumably continue branching.

The proximal-most columnal is very thin. Distally, the columnal height increases. The distal-most column is not present.

Material examined.– The holotype of *Trypherocrinus adamsensis* is OSU 50496.

Discussion.– *Trypherocrinus adamsensis* apparently has three basals, including one triangular plate formed by the fusion of EA and DE basal plates that articulates with

the radial circlet. The anal X is a pentagonally shaped plate supported beneath on one side by the B superradial and presumably on the other side by at least the C superradial. The anal X supports four additional anal plates. Thin proximal columnals are present. The distal portion of the column and holdfast are not present. *Trypherocrinus brassfieldensis* has three basals. The crown and aboral cup are relatively small. The E inferradial widens, distally to proximally. The E inferradial-basal circlet articulation forms approximately 70% of the radial-basal circlet plate articulation. The E superradial has a triangular shape. The anal X is a pentagonally shaped plate supported beneath on one side by the B superradial and on the other side by both the C superradial and the C inferradial. The anal X supports a single additional anal plate which is triangular. The proximalmost columnal is thin, elliptical and has a circular lumen. Distal columnals are disc-shaped. The holdfast appears to be composed of slightly larger columnals that penetrated vertically into the sediment. The distal, buried portion of the column is separated from the remainder of the column by a series of three wedge-shaped columnals. *Trypherocrinus adamsensis* and *Trypherocrinus brassfieldensis* lack the normal bilateral calceocrinid heterotomy, but they have nearly isotomous branching with a tendency toward adaxial heterotomy branching above at least the alphabrachials. Overall, arm branching patterns are nearly the same but with different locations of the axillary brachials. All basal plates of *Trypherocrinus* sp. are fused into one basal plate. The crown and aboral cup are medium-sized. The E inferradial pinches and swells, distally to proximally. The E inferradial-basal circlet articulation forms approximately 5% of the radial-basal circlet plate articulation. The E superradial is crescent in shape. The anal X is a pseudo-hexagonal shaped plate supported beneath on one side by both the B superradial

and the B inferradial and on the other side by both the C superradial and the C inferradial. The anal X supports two additional anal plates. Three thin, circular proximal columnals are present.

Occurrence.– Specimen found at a roadcut on the south side of Ohio State Highway 32, 0.9 km west of the intersection of Highway 32 with Unity Road, approximately 4.7 km east of Seaman. The location of this roadcut is 38˚55´35˝N lat., 83˚31´05˝W long., Oliver Township, Adams County, Seaman, Ohio, 7.5-min quadrangle. This specimen is from the Brassfield Formation (Aeronian, Llandoverian, Silurian), from the top of the section illustrated by Ausich and Dravage (1988, Fig. 1).

Measurements.– See table 1.

Etymology.– The species is named for Adams County, Ohio, where the specimen was collected.

***Calceocrinid* sp.**

Description.–The aboral cup is medium-sized, laterally compressed, and pendant on the stem.

The basal circlet is about half as wide as it is maximum height, with a roughly trapezoidal shape. All basal plates are fused into a single plate. The basal circlet is widest at its distal margin, and this plate edge forms most of the basal circlet margin.

The radial circlet is laterally compressed and rectangular from aboral view, and on a planar projection is roughly hexagonal. A and D radials comprise the majority of the radial plate circlet. Both the E inferradial and E superradial narrow in width toward the connection; the E superradial crescent in shape. The E inferradial-basal circlet

articulation forms approximately 5% of the radial-basal circlet plate articulation. The E superradial occupies the entire distal edge of the aboral cup and supports the E-ray arm. The upper lateral facet of the A radial supports the A lateral arm, and two lower lateral facets of the A radial support the B superradial and B inferradial. The upper lateral facets of the D radial support proximally the C superradial and inferradial and distally the D lateral arm. The B inferradial is larger than the B superradial which it supports on its distal abaxial boundary. The C inferradial is larger than the C superradial which it supports on its abaxial boundary.

The anal X is a pseudo-hexagonal plate supported beneath on one side by both the B superradial and the B inferradial and on the other side by both the C superradial and the C inferradial. The anal X supports two additional anal plates.

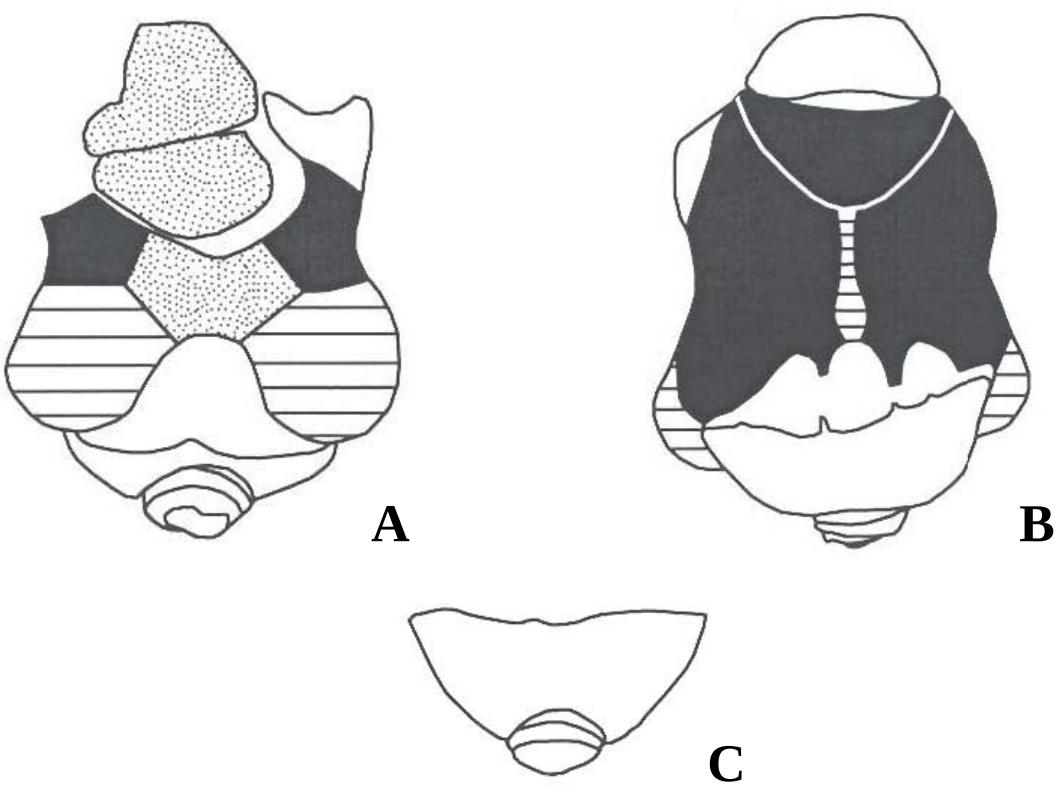
The proximal-most columnals are thin and circular. Three proximal columnals are present.

Material examined.– *Calceocrinid* sp. is known from one specimen, Cincinnati Museum Center 51205.

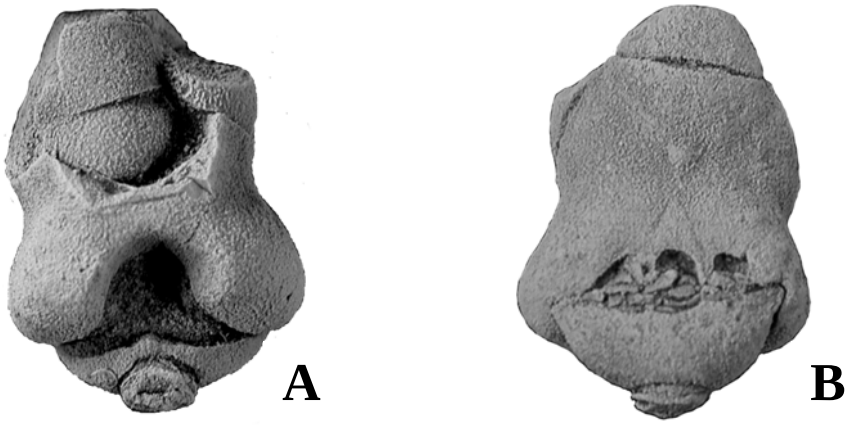
Discussion.– *Trypherocrinus* sp. has all the basal plates fused. The aboral cup is medium-sized. The E inferradial pinches and swells, distally to proximally. The E inferradial-basal circlet articulation forms approximately 5% of the radial-basal circlet plate articulation. The E superradial is crescent in shape. The anal X is a pseudo-

TABLE 2. Measurements of *Calceocrinid* sp. (in mm). Abbreviations same as in Table 1.

Specimen	HBC	WBC	HRC	WRC	HC	LC
CMC 51205	1.5	5.3	5.7	6.4	–	0.4*



TEXT-FIG 11. *Calceocrinid sp.*, holotype, Cincinnati Museum Center 51205, ×7.2. Camera lucida drawing; A, abanal view of aboral cup; B, adaxal view of aboral cup; C, adaxal view of basal circlet. Interpretation of plates same as TEXT-FIG 10.



TEXT-FIG 12. *Calceocrinid sp.*, holotype, Cincinnati Museum Center 51205, ×7. A, abanal view of aboral cup; B, adaxal view of aboral cup.

hexagonal shaped plate supported beneath on one side by both the B superradial and the B inferradial and on the other side by both the C superradial and the C inferradial. The anal X supports two additional anal plates. Three thin, circular proximal columnals are present. *Trypherocrinus brassfieldensis* has three basals. The crown and aboral cup are relatively small. The E inferradial widens, distally to proximally. The E inferradial-basal circlet articulation forms approximately 70% of the radial-basal circlet plate articulation. The E superradial has a triangular shape. The anal X is a pentagonally shaped plate supported beneath on one side by the B superradial and on the other side by both the C superradial and the C inferradial. The anal X supports a single additional anal plate which is triangular. *Trypherocrinus adamsensis* apparently has three basals, including on triangular plate formed by the fusion of EA and DE basal plates that articulates with the radial circlet. The anal X is a pentagonally shaped plate supported beneath on one side by the B superradial and presumably on the other side by at least the C superradial. The anal X supports four additional anal plates.

Occurrence.– Specimen found at a roadcut on I-64 near mile marker 121, Bath County, Kentucky. This specimen is from 3 m above the base of the Brassfield Formation (Aeronian, Llandoverian, Silurian).

Measurements.– See table 2.

REFERENCES

Ausich, W. I., 1984, Calceocrinids from the Early Silurian (Llandoverian) Brassfield Formation of southwestern Ohio: Journal of Palaeontology, v. 58, p. 1167-1185.

Ausich, W. I., 1986, Palaeoecology and history of the Calceocrinidae (Palaeozoic Crinoidea): Palaeontology, v. 29, p. 85-99.

Ausich, W. I., and Dravage, P., 1988, Crinoids from the Brassfield Formation of Adams County, Ohio: Journal of Paleontology, v. 62, p. 285-289.

Baumiller, T. K., 1992, Importance of hydrodynamic lift to crinoid autecology, or, could crinoids function as kites?: Journal of Paleontology, v. 66, p. 658-665.

Breimer, A., and Webster, G. D., 1975, A further contribution to the paleoecology of fossil stalked crinoids: Koninklijke Nederlandes Akademie van Wetenschappen, Proceedings, Ser. B., v. 76, no. 3, p. 249-167.

Brett, C. E., 1981, Systematics and paleoecology of Late Silurian (Wenlockian) calceocrinid crinoids from New York and Ontario: Journal of Paleontology, v. 55, p. 145-175, 5 pl.

Brett, C. E., 1985, Pelmatozoan echinoderms on Silurian bioherms in western New York and Ontario: Journal of Paleontology, v. 59, p. 820-838.

Brower, J. C., 1966, Functional morphology of Calceocrinidae with description of some new species: Journal of Paleontology, v. 40, p. 613-634, pl. 75.

Brower, J. C., 1977, Calceocrinids from the Bromide Formation (Middle Ordovician) of southern Oklahoma: Oklahoma Geological Survey, Circular, v. 78, p. 1-28, 4 pl.

Eckert, J. D., 1984, Early Llandovery crinoids and stelleroids from the Cataract Group (Lower Silurian), southern Ontario, Canada: Royal Ontario Museum Life Sciences, Contributions, no. 137, p. 1-83, 10 pl.

Jaekel, O., 1918, Phylogenie und System der Pelmatozoen: Paläeontologische Zeitschrift, v. 3, no. 1, p. 1-128. (Often referred to as 1921 but actually published October, 1918 and not reprinted 1921.)

Kesling, R.V., and Sigler, J.P., 1969, *Cunctocrinus*, a new Middle Devonian calceocrinid crinoid from the Silica Shale of Ohio: University of Michigan Contributions from Museum of Paleontology, v. 22, p. 339-360, 1 pl.

Macurda, D. B. and Meyer, D. L. 1974. Feeding posture of modern stalked crinoids. *Nature, Lond*. v. 247, p. 394-396.

Moore, R. C., 1962, Revision of Calceocrinidae: University of Kansas Paleontological Contributions, Echinodermata Article 4, p. 1-40, pl. 1-3.

Paleobiology Database. http://paledb.org/cgi-bin/bridge.pl Last accessed on July 9, 2007.

Ringueberg, E.N.S., 1889, The Calceocrinidae. A revision of the family, with descriptions of some new species: Annals of the New York Academy of Science, v. 4, p. 388-408, pl. 10-11.

Springer, F., 1926, American Silurian Crinoids: Smithsonian Institution Publication, 2872, p. 1-239, 33 pl.

Webster, G. D., 2003, Bibliography and Index of Paleozoic Crinoids, Coronates, and Hemistreptocrinoids: Geological Society of America, Special Paper, 363. http://crinoid.gsajournals.org/crinoidmod.

APPENDIX.– Data collected from Webster (2003) and the Paleobiology Database.

Period	Epoch	Age	Group	Formation
Ordovician	Late	Cincinnatian	Maquoketa	Scales
Ordovician	Late	Cincinnatian		
Ordovician	Late	Maysvillian	Maquoketa	Fort Atkinson Limestone
Ordovician	Late	Rawtheyan	upper Drummock	
Ordovician	Late	Caradocian		Benbolt
Ordovician	Late	Shermanian	Galena	Dunleith
Ordovician	Late	Blackriveran		Bromide
Ordovician	Late	Blackriveran		Mifflin
Ordovician	Late	Blackriveran	Platteville	Grand Detour
Ordovician	Late	Blackriveran		Bromide
Ordovician	Late	Blackriveran-Rocklandian		Plattesville
Ordovician	Late	Rocklandian-Kirkfieldian	Galena	Guttenberg
Ordovician	Late	Rocklandian-Shermanian		Decorah (Shale)
Ordovician	Late	Chatfieldian		Lexington Limestone
Ordovician	Late			Cyrene
Ordovician	Middle			
Ordovician	Middle	Trentonian		
Ordovician	Middle	Trentonian		Kirkfield
Ordovician	Middle	Trentonian		Hull Limestone
Ordovician	Middle	Trentonian		Trenton
Ordovician	Middle	Trentonian		
Ordovician	Middle	Trentonian	Liskeard	Farr
Silurian	Pridoli			
Silurian	Pridoli			Keyser
Silurian	Ludlow	Gorstian		Kopanina
Silurian	Ludlow			Henryhouse
Silurian	Ludlow-Wenlock	Gorstian-Homerian		Klinteberg
Silurian	Wenlock	Sheinwoodian		Slite
Silurian	Wenlock	Sheinwoodian		Hogklint
Silurian	Wenlock	Wenlockian		Much Wenlock Limestone
Silurian	Wenlock	Wenlockian		Lockport

APPENDIX (Continued)

Silurian	Wenlock		Clinton	Rochester
Silurian	Wenlock			Laurel Limestone
Silurian	Wenlock			Waldron Shale
Silurian		Niagaran		Brownsport
Silurian	Llandovery	Llandoverian		Brassfield
Silurian	Llandovery			Cataract
Silurian	Llandovery			Manitoulin
Silurian	Llandovery			Cabot Head
Silurian	Llandovery	early Llandoverian		
Devonian	late Middle			Hungry Hollow
Devonian	Middle	Givetian		Cedar Valley
Devonian	Middle	Givetian	Traverse	Four Mile Dam
Devonian	Middle	Givetian		Traverse
Devonian	Middle	Givetian-Eifelian		Alpena
Devonian	Middle	Givetian-Eifelian		Cedar Valley
Devonian	Middle	Givetian-Eifelian		Sellersburg
Devonian	Middle	Eifelian		Freilingen
Devonian	Middle	Eifelian		Cedar Valley
Devonian	Middle	Eifelian		Onondaga Limestone
Devonian			Genesee	Tully Limestone
Devonian	Middle			Thunder Bay Limestone
Devonian	Early	late Emsian		Bolast
Devonian	Early	late Emsian		Ben an Arreun
Devonian	Early	Emsian		Zlichov Limestone
Devonian	Early	Emsian		Oriskany Sandstone
Devonian	Early	early Emsian		
Devonian	Early			Koneprusy Limestone
Devonian	Early	Pragian		
Mississippian		Meramecian		upper Warsaw

APPENDIX (Continued)

Mississippian		Osagean	Edwardsville
Mississippian		Osagean	Burlington Limestone
Mississippian		Osagean	Keokuk
Mississippian		Osagean	lower Warsaw
Mississippian		Chadian	Fort Payne
Mississippian		Chadian	Fort Payne
Mississippian		Chadian	Borden
Permian	Early	late Artinskian	

APPENDIX (Continued)

Members	Locality
Orchard Creek Shale	United States, Illinois
Girardeau Limestone	United States, Illinois
	United States, Iowa
	Scotland
	United States, Virginia
Sherwood	United States, Minnesota
Pooleville	United States, Oklahoma
	United States, Illinois
Briton	United States, Illinois, Wisconsin
Mountain Lake	United States, Oklahoma
Hidden Falls	United States, Illinois, Minnesota, Wisconsin
	United States, Illinois
Spechts Ferry	United States, Minnesota
Curdsville Limestone	United States, Kentucky
	United States, Missouri
Lebanon Limestone	United States, Tennessee
Trenton Limestone	United States, New York
Kirkfield crinoid beds	Canada, Ontario
	Canada, Ontario
	Canada, Ottowa
Proser Limestone	United States, Wisconsin
	Canada, Ontario
Decatur Limestone	United States, Tennessee
	United States, West Virginia
	Czech Republic, Bohemia
	United States, Oklahoma
	Sweden, Gotland
	Sweden, Gotland
	Sweden, Gotland
Dudley Limestone	England
Gasport Limestone	Canada, Ontario

APPENDIX (Continued)

Lewiston	United States, New York
	United States, Indiana
	United States, Indiana
	United States, Tennessee
	United States, Ohio
Manitoulin Beds	Canada, Ontario
	Canada, Ontario
	Canada, Ontario
Gasworks Mudstone or Sandstone	England, Wales
	Canada, Ontario
Davenport Beds	United States, Iowa
lower Dock Street Clay	United States, Michigan
Silica Shale	United States, Ohio
	United States, Michigan
Littleton	United States, Iowa
	United States, Indiana
Nollenbach	Germany, Eifel
Linwood	United States, Iowa
	United States, New York
	United States, New York
	United States, Michigan
	France, Armorican Massif
	France, Armorican Massif
	Czech Republic, Bohemia
Ridgeley Sandstone	United States, West Virginia
Hunsrück Slate	Germany, Bundenbach
	Czech Republic
Dvorce-Prokop Limestone	Czech Republic, Bohemia
	United Sataes, Missouri

APPENDIX (Continued)

	United States, Indiana
	United States, Iowa
	United States, Iowa, Illinois
	United States, Iowa, Illinois
	United States, Kentucky
	United States, Kentucky
New Providence Shale	United States, Kentucky
Sargin Horizon	Russia, Krasnoufimsk

APPENDIX (Continued)

Environment	Collection Number
carbonate shelf	382, 26684
carbonate shelf	
carbonate shelf	23524
deep subtidal ramp	
deep subtidal ramp	
carbonate shelf	23477
deep subtidal ramp	24097, 24103
carbonate shelf	
carbonate shelf	23436
carbonate shelf	23990, 24102
carbonate shelf	23390
carbonate shelf	23457
carbonate shelf	23402
deep subtidal ramp	
carbonate shelf	
deep subtidal ramp	
carbonate shelf	
carbonate shelf	
carbonate shelf	
deep subtidal ramp	
carbonate shelf	
carbonate shelf	
carbonate shelf	
carbonate shelf	26695
reef, bioherm	
deep subtidal ramp	528, 26823, 26824
carbonate shelf	13602
carbonate shelf	13598
reef, bioherm	
deep subtidal ramp	
reef, bioherm	

APPENDIX (Continued)

offshore siliciclastic	12932, 13050, 13051
carbonate shelf	26700, 26771
offshore siliciclastic	26787, 26789, 26792, 26794
mixed carbonate/siliciclastic	
shallow reef, reef associated	
carbonate shelf	
reef, bioherm	
prodelta	3489
offshore siliciclastic	
mixed carbonate/siliciclastic	
carbonate shelf	
deep siliciclastic	
deep siliciclastic	55606, 66054
mixed carbonate/siliciclastic	
carbonate shelf	
carbonate shelf	
carbonate shelf	
carbonate shelf	
carbonate shelf	
carbonate shelf	
carbonate shelf	
carbonate shelf	
deep siliciclastic	
deep subtidal ramp	
shallow siliciclastic	
deep siliciclastic	
reef, bioherm	
mixed carbonate/siliciclastic	14136
deep siliciclastic	

APPENDIX (Continued)

siliciclastic delta	557
carbonate ramp	
carbonate ramp	
deep siliciclastic	
deep siliciclastic	
deep-water bioherm	2675, 2681
prodelta	5869
offshore siliciclastic	